

The University of Chicago

SIZE OF BREEDING POPULATIONS IN RELATION TO EGG-LAYING AND REPRODUCTIVE SUCCESS IN THE EASTERN RED-WING
(*AGELAIUS P. PHOENICEUS*)

A DISSERTATION SUBMITTED TO THE FACULTY OF THE
DIVISION OF THE BIOLOGICAL SCIENCES IN CANDIDACY
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOÖLOGY

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P. PHOENICEUS)¹

HARRY M. SMITH

Whitman Laboratory of Experimental Zoölogy, University of Chicago

The role of exteroceptive factors in relation to mating and reproductive success has long been a matter of interest. Much attention has been given to the biological significance of courtship patterns of behavior in many animals and particularly in birds (Whitman, '19; Matthews, '39 and citations). The apparently sound conclusion has been reached that such behavior has survival value (Howard, '29; Marshall, '36, '42). Studies of this nature received a new impetus from the growing recognition of the importance of animal aggregations in many phases of biology (Allee, '31; '38).

A few years ago Stresemann ('28, p. 407) found that small tern colonies produced a smaller percentage of offspring than did larger colonies and suggested that the larger colonies were more efficient in driving away marauding

gulls. More recently, Darling ('38) has focused attention upon the functional significance of the numbers present in breeding groups of birds by his observations upon herring gulls (*Larus a. argentatus*) and lesser black-backed gulls (*Larus fuscus affinis*). The findings and ideas of Darling will be reviewed briefly since they furnished the stimulus for and general orientation of the present study.

Darling recognized three effects of colony size upon breeding activities of these gulls. The larger colonies showed (a) an earlier beginning of laying, (b) a greater synchronization of breeding and (c) a higher reproductive success.

If we focus upon his most convincing data, viz., those for herring gulls in 1936, the findings were as follows: the largest colony of 84-90 gulls began laying on May 7 and finished on May 23, 17 days inclusive; 40 functional nests held 84 eggs which yielded 35 fledglings, a reproductive success of 42 per cent.

The second colony of 30-34 gulls started laying on May 12 and finished on June 3, 23 days inclusive; 12 functional nests held 26 eggs from which 8 (31 per cent) reached fledgling age.

The third colony of 20 birds began laying on May 18 and finished on June 12, 26 days inclusive; the 7 nests with eggs held 16 eggs from which 3 chicks (19 per cent) were fledged.

The fourth colony of 4 gulls did not build nests until after May 26 and laid no eggs.

Darling interpreted these results, together with a review of pertinent literature, to mean in general terms and in part as follows (p. 76): "I suggest that in birds social at the breeding season, the importance of synchronization ex-

¹ The present paper is based on a doctor's dissertation (see bibliography) which has been entirely rewritten for publication. The original manuscript is on file in the libraries of the University of Chicago and may be consulted for additional details. I wish to express my gratitude to Dr. W. C. Allee who originally suggested this problem and under whose direction it has been conducted. I am especially grateful to him for his aid in revising the manuscript for publication after my induction into military service. I am also indebted to Dr. Thomas Park for his immediate supervision of the work during the summer of 1939. Thanks are extended to Dr. Charles E. Olmsted and to Mr. Karl P. Schmidt for identifications; to Dr. Victor H. Dropkin for photographic assistance and for aid in the field; to Mr. Kenji Toda for drawing the graphs; to Mr. Asher J. Finkel for aid with statistical analyses; and to Mr. Rudyerd Boulton and Mrs. Margaret M. Nice for helpful advice and criticism. Much of the work was done while the writer held a Robert Ridgway Memorial Fellowship at the University of Chicago.

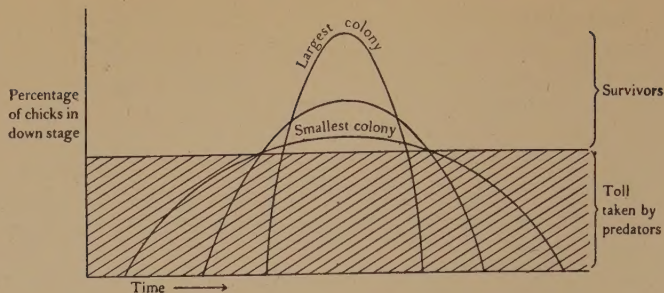


FIG. 1. A diagram which illustrates "how the survival rate is influenced by the 'spread' of time in which the eggs of a colony of herring gulls are laid."

tends to the ecological field of survival rate. That state is brought about by the same means of courtship display which synchronizes pairs of birds, but, in addition, the numbers of the flock are a potent factor because of the quantitative and cumulative value of their presence, general activity and courtship display. My observations show that as well as better synchronization of the breeding cycle, the onset of egg-laying is slightly earlier in the larger flocks. I do not suggest any particular survival value to rest in this phenomenon. . . ." Darling summarized his idea of the relation between synchrony of breeding and reproductive success in the diagram which is given here as figure 1.

These interesting observations and interpretations suggest two further types of investigation: In the first place, it is important to study intensively the relation between size of nesting colonies and onset of breeding, synchrony of breeding, and reproductive success in gulls and more or less closely related species in order to test for the generality of these phenomena among such birds in a variety of breeding locations. Second, tests are also needed concerning the universality of such relations among colonially nesting birds of many taxonomic ranks and ecological habitats. The present study is a contribution toward this second objective.

THE EASTERN RED-WING AS RESEARCH MATERIAL

The eastern red-wing was chosen for the present study for a number of reasons. As Mayr says ('41): "Red-wings can be considered, with certain reservations, to be colonial birds. We find that even in large marshes the nests are invariably clustered in a semi-colonial fashion." This species is found abundantly in the vicinity of Chicago as are the habitats in which it breeds. Many typical cat-tail (*Typha*) marshes exist which vary in size from a square rod or so to many acres in extent. Other marshy vegetation in which red-wings breed is also found nearby. A further reason for working with red-winged blackbirds came from the fact that many of its basic ecological relations are well known from the studies of Allen ('14), Mayr ('41) and others. I have relied much on the findings of these students, particularly upon Allen's work which was done at approximately the same latitude as Chicago. His observations have been verified at all points which were mutually touched at least as much as might reasonably be expected considering the differences in locality and the probable seasonal variations. Allen's paper should be read, or reread, to get a background of general life history and ecological relations; an effort will be made to avoid restating any such matters in the present discussion.

The advantage furnished by red-wings and yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) for such studies has been appreciated by others. Since the present study was begun, Mayr ('41) has published data showing that in contrast to Darling's findings with gulls, egg laying may start earlier in smaller colonies of red-wings than in larger ones. And Fautin ('41a) has evidence that the yellow-headed blackbird had greater nesting success in the larger of two colonies studied.

Throughout, the number of males in a given habitat was determined by counting individuals that had established territory. The number of females in the larger colonies was estimated by counting nests.

In beginning the study, the summer of 1939 was spent in a reconnaissance of many available cat-tail and other breeding localities in the vicinity of Chicago. During 1940 a preliminary investigation of the breeding localities was conducted over a three-month period which extended from the middle of March until the middle of June in localities which were selected for intensive study. Because of retarded red-wing breeding in this year, a complete analysis of their reproduction in the various marshes was not obtained. In 1941, however, an investigation of the 1940 as well as a few new study localities was begun during March and continued through August. In this year the writer took up residence near the localities which were to be investigated, and made intensive observations from the middle of April until the end of July. An automobile was used to travel between certain marshes which were far apart.

DESCRIPTION OF STUDY LOCALITIES

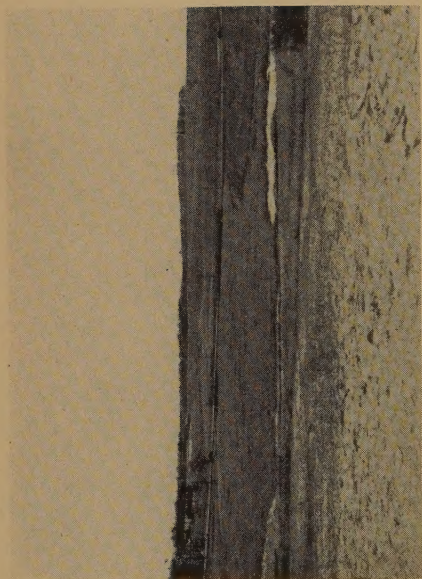
The reproduction of red-wings was followed in detail in 25 localities in the south-western part of Cook County, Illinois. Table I shows the number of individuals which bred in each of these study localities during 1940 and 1941.

The largest of these marshes (Locality 22c) consisted of approximately 5 acres and was located immediately north of Illinois highway 7 on the Orland Wildlife Refuge in the vicinity of Orland Park, Cook County, Illinois. A dense growth of cat-tails (*Typha latifolia* and *Typha angustifolia*) comprised the principal type of vegetation (pl. Ia). An irregular fringe of bulrushes (*Scirpus fluviatilis*) and bur reeds (*Sparganium eurycarpum*) grew about the periphery of the cat-tails. There were relatively few openings in the marsh, although a narrow channel of open water extended along the eastern margin. Drainage through the marsh was in a south-easterly direction, and thence by means of an intermittent creek into McGinnes Slough, an extensive, shallow body of water in the vicinity. Other more extensive cat-tail marshes occur relatively nearby which are more directly associated with the McGinnes Slough complex. The birds in Locality 22c will be referred to as group A or the colony at Orland.

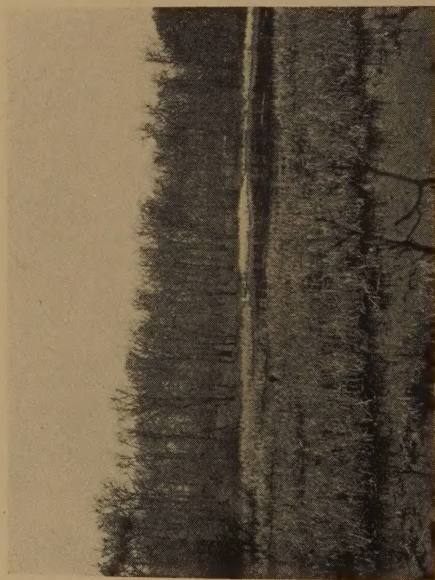
The 24 smaller localities were located in three general areas. Eighteen were on the extensive property of the Fifth Forest Preserve District of Cook County near Sag Bridge and Orland Park; the remainder were on private property. Only 19 of the 24 localities were studied in 1940. These localities and their inhabitants will subsequently be known as the marshes or red-wings of group B. Again the populations are summarized in table I both in general and in detail.

The Tinley Creek Woods area is located on fairly level ground near the eastern border of the Valparaiso moraine. Eight adjacent ponds and marshes, which were well-isolated from any other red-wing breeding localities, were present in this area. Cat-tails comprised the vegetation of two of these marshes. The nesting cover in one pond consisted of bulrushes. A summer-dry pond supported marginal vegetation of cat-tails and bur reeds on opposite shores. One locality was a marshy depression in

PLATE I



a. Locality 22c.



b. Locality 319b.



c. Locality 3a.

Photos by Dr. Victor H. Dropkin.

TABLE I. *Adult populations of study localities in groups A and B during the breeding seasons of 1940 and 1941*

Locality	Cover	1940		Completed nests	1941		Completed nests
		♂ ♂	♀ ♀		♂ ♂	♀ ♀	
Group A							
Orland Wildlife Refuge							
22c	<i>Typha</i>	??	122	128	40+	about 110	167
Group B							
Tinley Creek Woods area							
29bs	<i>Typha</i> and <i>Sparganium</i>	1-2	2	2	1	2	4
29bt	<i>Sparganium</i>	0	0	0	1	1	1
29bu	<i>Cephalanthus</i>	1-2	?	0	1	1	2
29bv	<i>Typha</i>	1	1	1	1*	1*	2
29bw	<i>Sparganium</i>	1	1	1	2	4	6
29bx	<i>Cephalanthus</i>	2	3	3	1	2	4
29by	<i>Typha</i>	4	8	8	3	11	24
29bz	<i>Scirpus</i>	1	2	2	1	2	3
Bell Road area							
28a	<i>Typha</i>	1-2	?	0	0	0	0
28b	<i>Typha</i> and <i>Sparganium</i>	2-3	6-7	9	1	2	3
528b	<i>Sparganium</i>	1	1	2	0	0	0
528c	<i>Typha</i>	3-4	10-11	14	1	1	1
320a	<i>Typha</i>	—	—	—	1	2	3
Red Gate Woods area							
30a	<i>Scirpus</i>	1	3	3	1	2	3
30b	<i>Typha</i>	4	11	11	5	15-17	24
30c	<i>Typha</i>	0	0	0	1	2	2
320b	<i>Solanum</i>	—	—	—	1	1	1
528a	<i>Cephalanthus</i>	1	2	3	1	1	2
428a	<i>Typha</i>	2-3	4	6	2	6	8
324a	<i>Typha</i>	—	—	—	5	19	25
321a	<i>Typha</i>	—	—	—	1	1	3
Mount Forest Island area							
319b	<i>Typha</i>	—	—	—	8-12	34	57
513a	<i>Typha</i>	2	6	7	1	3	6
3a	<i>Typha</i>	1	3	3	3	3	5
Total of study localities in B		29-35	63-65	75	42-46	115-117	189

* This pair of individuals is identical with the pair of Locality 29bt. The male maintained a territory which comprised both of these adjacent ponds; and the female interspersed an unsuccessful nesting attempt in Locality 29bt between two nestings, both of which were also unsuccessful, in Locality 29bv.

which there was a fair growth of *Sparganium*, and one was a permanent pond which was fringed with bur reeds. The remaining two localities were brushy ponds in which there was a vegetation of buttonbushes (*Cephalanthus occidentalis*).

Five marshes and ponds were located in fairly close proximity on private property in the Bell Road area near Sag Bridge, Illinois. There were no other nesting red-wings within approximately 350 yards. These habitats were

shallow depressions in a cattle pasture, and were situated on glacial till of the Valparaiso moraine. Cat-tails comprised the principal type of vegetation in four of these marshes; a clump of bur reeds also contributed to the nesting cover in one locality and a restricted growth of these reeds in a pond was the fifth nesting habitat in this area. Cattle trampled and grazed upon the aquatic vegetation of these marshes during the dry summer of 1940. As a consequence,

there was, throughout the breeding season of 1941, very little cover provided by standing vegetation of the preceding year. It was not until the middle of May that the growing vegetation of 1941 was sufficiently dense to provide adequate cover for any nests. And since the height of early reproduction in the study area had already begun to decline at this time, the total red-wing population here was much lower in 1941 than in the preceding year.

Eight marshes and ponds were situated in the Red Gate Woods area near the western edge of Mount Forest Island in a region of low red-wing density. Mount Forest Island is a knob and kettle remnant of an insular area during an earlier epoch in the history of recession of Lake Michigan. The density of population of red-wings becomes progressively higher in an easterly direction. Cat-tails grew in five of these marshes. In one pond the nesting cover consisted of bulrushes. A thicket of buttonbushes was present in another pond and the eighth breeding habitat was a moist depression in which the vegetation consisted of bittersweet shrubs (*Solanum dulcamara*). During 1940 only five of these localities were studied, in one of which no red-wing reproduction occurred. In 1941 all eight of the localities were populated with a total of 17 males and 48 females.

One of the three remaining habitats was located in an easterly direction in the central part of Mount Forest Island. This marsh, known as Locality 319b, was unstudied in 1940. It was an open-water pond of intermediate size which supported a fairly dense growth of cat-tails along its margins (pl. Ib). Its 1941 population of 8-12 males and 34 females was the largest of these smaller breeding aggregations of red-wings. The second locality, a cat-tail depression, was located farther east in the vicinity of a larger, unstudied pond fringed with the same type of vegetation. The third locality (pl. Ic) was a small, mature

Typha marsh located on private property near the eastern edge of Mount Forest Island.

POPULATION SIZE

Without data for a much longer period, it is impossible to estimate the numbers which these habitats can carry or to discuss the recorded populations in relation to minimal, optimal or maximal breeding populations. The weather for 1940 and 1941 differed greatly. The former year was much colder during April and early May and nesting was accordingly retarded. Yet the number of red-wings present was of the same order of magnitude for the two years. Thus, as shown in table I, 122 females built 128 early nests at Orland in 1940 as compared with about 110 females which constructed 131 nests in brood I for 1941.

Of the B marshes which were studied in both years, where conditions were comparable the total populations were 68-71 adults for 1940 (50 nests) as compared with 79-81 for 1941 (84 nests). In getting these figures the marshes in the Bell Road area were omitted because of changed physical conditions. If they are included, the figures become 92-100 for 1940 (75 nests) against 84-86 for 1941 (87 nests). This indicates that there was no great difference in size of breeding populations in these localities for these two years.

OUTLINE OF STUDY

The present investigation is a comparative study of the beginning of breeding, the temporal spread of egg-laying, and reproductive success in (1) an extensive breeding colony of red-wings (group A) and (2) an equivalent number of individuals breeding in limited groups throughout the area (group B).

Table I shows that in 1941 there were fewer than ten adults per locality in 18 and fewer than five adults in 15 of the 22 inhabited marshes of group B. In

1940, only 4 of the 17 occupied breeding habitats contained as many as 10 adults each. Groups A and B thus constitute two numerically equivalent populations which differ (1) in numbers of red-wings breeding in the given habitats, (2) in size of habitat which is suitable for red-wing nesting, (3) in duration of suitability and (4) in type of nesting cover. The data which are discussed in the present paper have been analyzed, upon a comparative basis, primarily with respect to variation in size of breeding colony between these two groups of individuals. The habitat differences between the two are not entirely neglected. Further work is needed before the differences in physical or plant characteristics of the habitats can be properly evaluated.

METHODS

The procedure used throughout the study was to tag nests. This was usually done during an early or intermediate stage of nest construction. In 1940 numbered adhesive-tape labels were used. During 1941, tags were nearly all made of galvanized sheet steel, on which a number had been stamped; a few adhesive labels were also used. The tag was attached in an inconspicuous position on the supporting vegetation of the nest. In 1941 the nests were usually visited no less frequently than on alternate days, and pertinent data were recorded in field notes. These were transferred to more permanent records at the conclusion of the study.

Insufficiency of time in relation to an extensive analysis of numerous red-wing breeding populations prohibited any banding studies in the present investigation. The need for this added refinement was recognized from the beginning. Every allocation of a nest with respect to its proper brood is therefore based entirely upon the spatial and temporal distribution of the various nests in question. As Allen ('14, p. 95) states, a nest of a double-brooded female is

constructed in the immediate vicinity, and frequently within a distance of ten feet, of an original nest; this also applies to renestings which follow completely unsuccessful original nestings. Allen's method of correlation between an original nest, a renest following disturbance or destruction of the first, or a second nest in the case of double-brooded females is considered to be a fairly adequate basis upon which to establish these relationships. More precisely, a new nest was recorded as a renest if it was first discovered in the field shortly after the destruction of an earlier nest which had been built in the immediate vicinity. Similarly a new nest was recorded as a nest of brood II if it was built nearby immediately following the departure of young or while young were in an advanced stage of development in the original nest.

In this paper total figures for time relations of egg-laying and for reproductive success will be stressed. The more obvious indications will also be presented for broods I and II in groups A and B. Little attempt is made here to break down data of any particular brood into original nestings and renestings. The analyses of this sort which were tried in a preliminary fashion in no way modify the general results.

The area of every study locality was found by tracing outline drawings of commercially prepared aerial photographs of these marshes and ponds by means of a polar planimeter.² The extent of margin (edge) in these localities was obtained from these aerial photographs by running a map measuring wheel around an outline drawing of the periphery of every locality and around the margins of its openings. Such figures of edge are necessarily approximations since the boundaries of openings in a marsh are frequently difficult to

² The scale of these photographs was approximately 1 inch per 144 feet for the marsh at Orland, and 1 inch per 262 feet for the other 24 marshes and ponds.

distinguish in an aerial photograph and since highly precise readings of linear distances cannot be obtained with a map measuring wheel of the sort which was used in this work. In addition, the boundaries of many of the margins varied as the season progressed.

A knowledge of the date on which every egg was laid in 1941 has provided the basis for determining the beginning and the span of egg laying in the two major categories of individuals. Reproductive success has been based upon the number of nestlings which were fledged as juveniles, and was determined by following each nest until after the nestlings had left the nest, or until after mortality had occurred. Usually it was fairly easy to follow in a general way the history of each nest. For example, infertility of eggs was easily recognizable as such. Destruction of eggs or nestlings by predators was also distinguishable from death following desertion of eggs or trampling of nests by cattle. Table II represents an analysis of these factors of mortality in groups A and B during

the breeding season of 1941. Of the various types of mortality, predation of eggs and nestlings contributed the highest percentages in both groups of individuals.

In cases of predation it was usually difficult to determine the species of predator inasmuch as relatively few instances of this type of mortality were actually witnessed. Bluejay and crow feathers were found near nests in which eggs had been destroyed and a snake identified as *Elaphe v. vulpina* is known to have inhabited one marsh. Flocks of grackles and starlings roosted in certain of the marshes during early spring, but there is no evidence of their role as predators. Unidentified mammalian faecal pellets were found in one nest.

ESTABLISHMENT OF TERRITORIES AND NEST BUILDING

The establishment of territories at Orland in 1941 began during the middle or latter part of March and continued into early April. Territories were established in certain of the marshes and ponds of group B as early as at Orland. However, this process continued further into April in a few of the restricted localities of this group than at Orland. Possibly this is related to an inhabitation of certain of these localities by young males. At least males with duller brownish feather tips both on body and wing coverts were seen to take up territories in these smaller marshes during April. Such individuals supposedly migrate later in the spring than do older resident adult males (Allen, '14, p. 86, p. 95). The arrival of resident female individuals began during early April. Sexual chasing and other aspects of courting were conspicuous during the middle of April at which time nest building was begun.

In early spring as many as 7 days may pass after completion of a nest before eggs are laid; subsequently the interval is shortened to one or two days.

TABLE II. Causes of mortality in groups A and B during the breeding season of 1941

	A		B	
	No.	%	No.	%
Total number of eggs laid	563		577	
Egg loss				
1. Elemental				
a. Wind.....	4	1.8	5	2.1
2. Biotic				
a. Growth of vegetation.....	0	0	3	1.3
b. Predation.....	87	38.3	120	51.1
c. Death of adults	15	6.6	9	3.8
3. Physiological				
a. Infertility.....	19	8.4	18	7.7
b. Loss at hatching.....	12	5.3	9	3.8
c. Desertion.....	8	3.5	5	2.1
d. Egg-removal.....	0	0	3	1.3
Total eggs lost.....	145	63.9	172	73.2
Nestling mortality				
1. Elemental				
a. Drowning or exposure.....	8	3.5	0-1	.2
2. Biotic				
a. Predation.....	70-72	31.3	56-59	24.5
b. Trampling of nests by cattle	0	0	3	1.3
3. Physiological				
a. Mortality at hatching.....	2	.9	1	.4
b. Starvation.....	1	.4	1	.4
Total nestling mortality.....	81-83	36.1	61-65	26.8
Total mortality.....	226-228	100	233-237	100

In part, the developing sequence is broken by introducing the following details at this point. However, they have an important bearing on the date of onset of given reproductive activities in the large breeding population at Orland as contrasted with the smaller groups of red-wings and should be presented here. In 1940 red-wing breeding was held up by a cold and retarded spring, and no nests were found in any locality on May 4. On May 6 at Orland, there was one completed nest without eggs. Eggs were laid in this nest on May 14, 15, 16 and 17, one egg each day as is usual in this species. The first nestlings were seen on May 29 when there were three young and one egg in the nest. Hatching probably occurred on May 28.

In comparison, among the marshes of group B, the first nest in 1940 was found on May 12 in marsh 3a. It contained one egg and may have been completed as early as the first nest at Orland. Eggs were laid on May 12, 13 and 14 and all three eggs hatched probably on May 25; three young were present on May 31. This set of eggs and nestlings preceded the earliest ones in the large colony. Locality 3a contained 4 adults.

In 1941 nests were frequently visited daily during early spring, and for these early nests and under these circumstances, the interval between observations was never greater than two days. The following sequences of first observations were recorded:

At Orland, the first nest was found on April 16 (it may have been begun on the preceding day); first egg, April 21; first nestling, May 4 (probably hatched on May 3); first fledgling, May 14 or 15.

Among the B marshes, the first nest was in Locality 3a and was found on April 17. It may have been begun on April 16. The first egg was laid on April 23; first nestlings, May 6 (3 young plus 1 egg) or May 7 (4 young). Two young had left the nest on May 17; they could have left on May 16. There

was an adult population of 6 birds in this nesting population.

Thus in 1940, egg laying and development up to the fledgling stage was slightly ahead in one of the smaller breeding colonies; in 1941, the larger colony was 1 or 2 days ahead. Both differences were slight and probably lack significance. It is interesting to note that in 1941, the first female to deposit eggs in the B marshes, laid her clutch of eggs on April 23, 24, 25 and 26 and no other female began laying until April 30. Hence, this one bird aside, the onset of general egg laying started considerably later in the scattered marshes than it did in the large colony at Orland.

EGG-LAYING

The present data concerning egg-laying are based upon eggs which were deposited in nests in the study localities during 1941. The data for 1940 are excluded because they were not collected frequently enough and because field work had to be discontinued before the breeding season was concluded.

When the total time span for ovulation in groups A and B is considered (figure 2), it is seen that the least synchronous span of ovulation was that of the breeding colony of greatest magnitude. Egg-laying, in group A, began two days earlier in April and was protracted further into July than in any or all of the restricted localities in group B. As figure 2 shows, egg-laying commenced at Orland (solid line) on April 21 and continued over an 83 day period which extended until July 12 with a series of four consistently diminishing peaks. The earliest of these peaks consisted of 38 eggs and was attained on May 9. A second peak on May 22 followed a general decline in egg production which culminated on May 20. This second peak represents renests of brood I that followed completely unsuccessful original attempts as well as a few original nestings of brood I and early original nests of

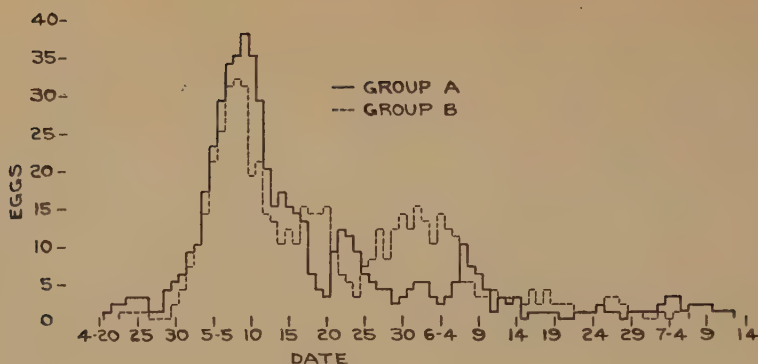


FIG. 2. Total span of egg-laying in groups A and B during the breeding season of 1941.

brood II.³ A third peak on June 7 is at the height of the initial nests of brood II. A slight rise in egg-laying early in July is more difficult to explain; it was originally believed to be a result of triple-broodedness and may in fact represent this phenomenon.⁴ In order to be conservative, these will be referred to as the July eggs or brood.

In group B (broken line) egg-laying

³ Double-broodedness in *A. phoeniceus* is well known and has been discussed at length by Allen ('14). It is possible that a few of the nests which were assigned in the field to brood II in reality belong to brood I. They may have been constructed by immature females which are supposed to migrate and breed later than older resident adult females (Allen, '14, p. 86).

⁴ Triple-broodedness is well known for this species in the southern part of its breeding range; it has been recorded near Ypsilanti, Michigan by Peet ('08, p. 165) who states that "two or three broods are usually raised." The presence of a third brood at Orland in 1941 is not conclusively indicated by available data. The nests which were built during July may represent (a) original nests of brood I for resident immature females; (b) re-nests of late nesting females in brood I; (c) original nests of brood II of females which had previously nested elsewhere in the area and then shifted into the marsh at Orland following the drying up of their former habitats. Intensive banding operations are needed to test critically this matter of triple-broodedness in red-wings in northern Illinois. The nests in this July brood were not closely related to any earlier nests. In general they were distributed about the few remaining areas of open water which extended along the eastern margin of Locality 22c.

began on April 23 and extended over a 75 day period which ended on July 6 (figure 2). There were three general peaks of egg-laying. The highest of these peaks, which represents eggs of original nestings of brood I, comprised 31 eggs and was reached on May 8. A lesser peak, only partially separated from the preceding peak, extended from May 17 to May 20; it consisted primarily of re-nestings of brood I which followed completely unsuccessful original nestings. A third broad peak during the end of May and early part of June represents re-nestings of brood I and original nestings of brood II. There was no evidence of a rise in egg-laying during July.

The earliest onset of reproduction in the largest colony in 1941 is in accordance with Darling's findings in gulls. The prolongation of egg-laying into the fall end of the breeding season in group A appears superficially to indicate a lesser synchrony of egg-laying in the largest colony and this is in contrast to Darling's observations for gulls. However, as has already been mentioned, this continuation of reproduction is correlated with other conditions which made interpretation difficult. In order to obtain a better understanding of the facts, it may be helpful to break down the observations in terms of field estimates concerning original nestings and

renestings of the different broods in the two major categories of individuals.⁵

The adult population of about 110 females which constructed 131 nests of brood I at Orland deposited 455 eggs over a 45 day period which extended from April 21 until June 4 (figure 3). The peak was attained on May 9 when 38 eggs, 8.4 per cent of the total number of eggs of brood I, were laid. During a 7 day peak which extended from May 5 to May 11 a total of 223 eggs, 49.0 per cent of the eggs of nests of this brood, was deposited. On one day (May 30) of this 45 day span there were no eggs of brood I deposited in this locality. There is thus a period of only 39 days during which there was a daily deposition of one or more eggs allocated to this brood in this marsh.

In group B, the total number of 115-117 females which constructed 155 nests of brood I deposited 484 eggs over a 75 day period extending from April 23 to July 6 (figure 3). The peak was attained on May 8 on which day 31 eggs, 6.4 per cent of the total number of eggs of this brood, were laid. As at Orland, the seven most productive days in group B extended from May 5 to May

11. During this 7 day period, 176 eggs, or 36.4 per cent of the total number for brood I, were laid. There was a period of 43 days, extending from April 30 to June 11, during which a minimum of one egg was deposited every day in these localities. One early nesting female and one female which laid during July are primarily responsible for extending this period of egg-laying to 75 days. The later nests allocated to this brood were judged to be renestings following the destruction of the original set of eggs or nestlings.

Graph 3 indicates that the highest one-day peak of egg-laying in brood I was slightly higher in A than in B. Similarly, there was a 12.6 per cent higher 7 day peak of egg-laying in A than in B. The duration of egg deposition assigned to brood I was 30 days longer in B than in A. This is a rather convincing indication for this brood of a higher synchronization of egg-laying in the extensive colony of red-wings.

A somewhat different relationship exists between the spans of oviposition of brood II in the two groups of red-wings. In group A, 25 females, which constituted an incidence of double-broodedness of 22.7 per cent, deposited a total of 91 eggs in 30 nests allocated to brood II. The span of these ovulations (figure 4) extended over a 50 day period with a peak of 10 eggs (11.0 per

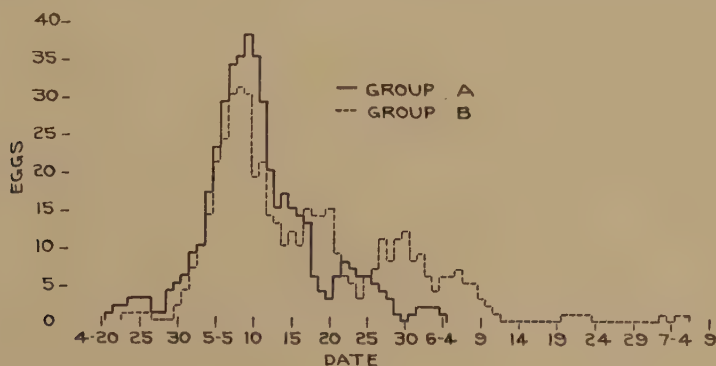


FIG. 3. Span of egg-laying of brood I in groups A and B during the breeding season of 1941.

⁵ There was very little doubt in assigning the majority of nests of this study to their proper broods. However, as has been mentioned earlier, an intensive banding investigation is the only critical method of correlating red-wing nests with their respective females.

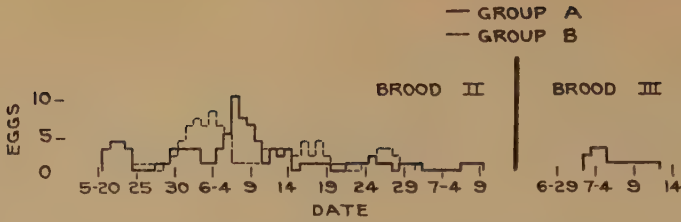


FIG. 4. Span of egg-laying of brood II and the July brood (III) in groups A and B during the breeding season of 1941.

cent) deposited on June 7. In B, 27 females, which constituted an incidence of double-broodedness of 23.3 per cent, deposited a total of 93 eggs in 34 nests of brood II. In this category, the span (figure 4) extends over a 37 day period with a peak of 8 eggs (8.6 per cent) on June 4. With respect to brood II, the peak of ovulation is again higher in A than in B, although there is a longer span of egg-laying at Orland than in B. This may well be an expression of a prolongation of satisfactory breeding conditions in the large marsh at Orland.

There were six females (see footnote 4) which may represent an incidence of triple-broodedness of 5.5 per cent at Orland during 1941. These six females deposited 17 eggs over a known 10 day period which extended from July 3 to July 12 (figure 4). As has been stated earlier, there was no evidence of a rise in egg-laying during July in group B.

By way of summary the following facts may be stated for the breeding season of 1941. (1) The least synchronous total span of reproduction was that of the breeding colony of greatest magnitude. (2) Egg-laying began earlier and there was a higher synchronization of the span of egg-laying of brood I in A than in B. This is in line with Darling's observations for gulls. (3) Again the peak of egg-laying of brood II was higher in A than in B. In this case there was a longer span of egg-laying in A. There were similar percentages of double-broodedness in A and B. (4) There was a slight rise in egg production during July in the large breeding marsh.

REPRODUCTIVE SUCCESS

A third suggestion of Darling's ('38) and one on which he placed much emphasis concerns the ecological survival value or relative breeding success of larger colonies of breeding birds. In the present discussion reproductive success is calculated in terms of the percentage of individuals which were fledged as juveniles in relation to the total number of eggs deposited. The figures of egg and nestling mortality similarly represent percentages of the total number of eggs which were deposited. No attempt has been made here to study the death rate among fledglings.

There is no real difference between the total percentages of reproductive success in the two categories of red-wings. In 1941, at Orland, there was a total of 563 eggs (5.12 per ♀) deposited throughout the breeding season (table III). Of this number, there was a loss of 145 eggs (25.7 per cent) and of 81-83 nestlings (14.6 per cent). These figures indicate

TABLE III. Total figures of mortality and reproductive success in groups A and B during the breeding season of 1941

	Fe- males	Eggs	Egg mor- tality	Nestling mortality	Repro- ductive success
Group A	about 110	563	145 25.7%	81-83 14.6±.18%*	335-337 59.7±.18%
Group B	115- 117	577	172 29.8%	61-65 10.9±.35%	340-344 59.3±.35%

* Percentage represents a mean figure wherever there is an uncertainty about the mortality or success of any nestlings; ± designates greatest error which may be added or subtracted in order to obtain limits of this discrepancy.

a total mortality of 40.3 per cent. Conversely, 335-337 individuals which were fledged as juveniles result in a total reproductive success of 59.7 per cent. Inasmuch as there was no July brood in B, it may be worthwhile to omit such eggs from consideration at Orland. Of 546 eggs deposited earlier, there was a loss of 137 eggs (25.1 per cent) and of 78-80 nestlings (14.5 per cent). This indicates a success of 60.4 per cent (table IV).

TABLE IV. *Mortality and reproductive success of broods I and II in group A during the breeding season of 1941*

	Fe- males	Eggs	Egg mor- tality	Nestling mortality	Repro- ductive success
Group A	about 110	546	137 25.1%	78-80 14.5 ± .18%	329-331 60.4 ± .18%

In group B a total number of 577 eggs (4.97 per ♀) was laid in broods I and II during the breeding season of 1941 (table III). In this group there was a mortality of 172 eggs (29.8 per cent) and 61-65 nestlings (10.9 per cent). Summing the percentages of these two gives a total loss of 40.7 per cent. A total number of 340-344 individuals which were fledged successfully indicate a reproductive success of 59.3 per cent.

These results were analyzed statistically. The value of P was obtained from formula 19.4 given by Yule and Kendall ('40, p. 360) for the standard error of the difference between two proportions. A P-value of .05 is approximately equal to 2x the standard error of such a difference and is here regarded as the upper limit of statistical significance.

There is no real difference between the respective percentages of total reproductive success in the two categories of individuals. A high value of 0.89 which was obtained for P is an expression of the statistical insignificance of this difference. The incidence of egg mortality in B is 4.1 per cent higher than in A. Conversely, however, there is a slightly

higher nestling mortality of 3.7 per cent in A than in B. If the data which pertain to the July eggs in A are omitted, the success of reproduction of the more highly comparable broods I and II is again insignificantly (1.1 per cent) higher in A than in B. P equals .69 in this analysis. These results give little or no support for a possible extension of Darling's hypothesis to reproductive success in the red-wing colonies studied.

An analysis of reproductive success in brood I of each category of individuals brings out further negative results with respect to Darling's hypothesis. At Orland, during 1941, a total number of 455 eggs was deposited in nests of brood I. Of this number, there was a mortality of 111 eggs (24.4 per cent) and 74-76 nestlings (16.5 per cent). The remaining 268-270 individuals which left nests as juveniles indicate a reproductive success of brood I of 59.1 per cent (table V). Incomplete results of 1940

TABLE V. *Mortality and reproductive success of broods I, II and III in groups A and B during the breeding season of 1941*

	Fe- males	Eggs	Egg mor- tality	Nestling mortality	Repro- ductive success
Brood I					
A	about 110	455	111 24.4%	74-76 16.5 ± .2%	268-270 59.1 ± .2%
B	115- 117	484	126 26.0%	48-52 10.3 ± .4%	306-310 63.6 ± .4%
Brood II					
A	25	91	26 28.6%	4 4.4%	61 67.0%
B	27	93	46 49.5%	13 14.0%	34 36.6%
July Brood					
A	6	17	8 47.1%	3 17.6%	6 25.3%

indicate a mortality of 17 of 65 eggs, an egg mortality of 26.2 per cent, in nests of brood I. As a result of the early termination of study during 1940, there are no data concerning nestling mortality or reproductive success in this group.

In B, corresponding data of 1941 indicate a total number of 484 eggs which were deposited in nests of brood I. Of these, there was a mortality of 126 eggs (26.0 per cent) and 48-52 nestlings

(10.3 per cent). A total of 306–310 individuals, or 63.6 per cent, were fledged successfully (table V). In 1940, partial results apply to a mortality of 26 of 115 eggs in nests of brood I. This gives an egg mortality of 22.6 per cent. Again, the data of this year are insufficient to establish any percentages of nestling mortality or total reproductive success in group B.

The success of reproduction of brood I during 1941 is thus 4.5 per cent higher in B. than in A. This difference lacks statistical significance (P equals .16). The important fact is that there is no indication of greater survival value related to the greater synchrony of egg laying for this brood at Orland.

When the success of brood II in groups A and B is considered, a distinctly different type of relationship is seen to exist between the two sets of populations. Out of 91 eggs of this brood in the large colony at Orland there was a mortality of 26 eggs and 4 nestlings (table V). The 61 individuals which were fledged indicate a success of 67.0 per cent. In the scattered marshes of B, on the other hand, there was a mortality of 46 eggs and 13 nestlings out of a total of 93 eggs (table V). This leaves only 34 individuals, or 36.6 per cent, which were fledged successfully. A very high egg loss of 49.5 per cent contributes heavily to the high total mortality figure of this brood in group B. Statistically the reproductive success of brood II is significantly higher in A than in B (P equals .00004).

Only 17 eggs were deposited in the July brood at Orland and only 6 individuals (35.3 per cent) were fledged. The success of this brood is thus very low although the sample is too small to be of much significance. However, it is to be compared with the complete absence of this brood in group B.

A few other analyses of reproductive success in the various marshes of B during 1941 may be helpful in studying any possible correlation between the

magnitude and relative success of a breeding colony. Locality 319b is an open-water pond of intermediate size which had a breeding population of 8–12 males and 34 females in 1941 (see table I). It is the largest of the 24 breeding colonies in B. A total of 178 eggs were deposited in 57 nests in this locality in broods I and II. Of these, there was a loss of 61 eggs (34.3 per cent) and of 16 nestlings (9.0 per cent). This leaves 101 individuals, or 56.7 per cent, which were fledged successfully. In the 23 remaining breeding populations of B there was, of 399 eggs deposited, a mortality of 111 eggs (27.8 per cent) and 45–49 nestlings (11.8 per cent). A total of 239–243 individuals which left nests successfully indicate a reproductive success of 60.4 per cent. The difference of 3.7 per cent is statistically insignificant (P equals .41).

Similarly, a comparison of the figures of reproductive success of broods I and II may be made in relation to a further re-arrangement of the localities of B. In this instance one grouping consists of Localities 319b, 324a, 30b, and 29by, each of which was populated by an excess of 10 adults; the other consists of the remaining 20 localities in which there were fewer than 10 adults in each breeding population. Of 398 eggs deposited in the four larger populations, there was a mortality of 122 eggs (30.6 per cent) and 42–43 nestlings (10.7 per cent). The total of 233–234 individuals which were fledged indicates a fledgling success of 58.7 per cent. In the remaining 20 localities, there was, of 179 eggs deposited, a mortality of 50 eggs (27.9 per cent) and 19–22 nestlings (11.5 per cent). The remaining 107–110 individuals which were fledged give a reproductive success of 60.6 per cent. The difference of 1.9 per cent lacks statistical significance (P equals .66).

The analysis of reproductive success in group B may be pushed a step further by distributing the 24 study localities among three minor groupings as follows:

(1) Locality 319b, the afore-mentioned marsh of intermediate magnitude, (2) Localities 324a, 30b, and 29by, three localities of fair magnitude, and (3) the remaining 20 localities in which, individually, there were fewer than 10 red-wings per locality. There is an absence of any direct correlation of reproductive success with the magnitude of breeding population in these various marshes. The figures are 56.7 per cent, 60.2 per cent and 60.6 per cent respectively. No real difference exists among these three figures or between any of them and the percentage of individuals (59.7 per cent) which left nests successfully at Orland during 1941.

Upon the basis of the present discussion the following conclusions may be drawn. (1) A negligible difference exists between the respective percentages of total reproductive success in groups A and B. (2) The reproductive success of brood I is statistically similar in the category of smaller populations (B) and in the large population at Orland. (3) There is a significantly higher success of reproduction of brood II in A than in B. (4) The success of the July brood at Orland is very low. (5) No obvious correlation exists between reproductive success and the magnitude of breeding population in various minor groupings of the study localities of B.

Reproductive success may also be analyzed from a somewhat different aspect, viz., that of the number of juveniles fledged per adult in the breeding population. Such an analysis for 1941 corroborates the conclusions just given. In A, 3.05 juveniles were fledged per adult female and 2.17 per adult male and female. This amounts to 2.01 fledglings for each completed nest. The corresponding numbers fledged for the scattered B populations were 2.95, 2.14, and 1.81 respectively. The smaller success per nest in B amounted to 0.20. None of the differences between A and B is impressive. In general terms, approximately the same breeding population in the two

categories under consideration" produced approximately the same number of offspring. The females in the smaller marshes constructed 22 more nests and hence had a slightly smaller reproductive success per nest which, however, is of no statistical significance. This method of analyzing reproductive success indicates clearly that the bulk of juveniles fledged during the breeding season are of brood I with 2.45 per female in A and 2.66 in B. The paucity of juveniles of brood II (0.55 per adult female in A in comparison with 0.29 in B) results primarily from a restricted incidence of double-broodedness in the adults of the marshes of the present region. The contribution of the July brood at Orland to the total number of juveniles is even less and amounted to only 0.05 per adult female of the original breeding population. This is, however, to be compared with an absence of any juveniles of this brood in B.

OTHER ASPECTS OF REPRODUCTION

Certain other data which have been analyzed in the present study concern (1) fecundity and fertility in *A. phoeniceus*, and (2) the incidence of intra-brood parasitism of red-wings by the eastern cowbird (*Molothrus a. ater*).

In determining fecundity only completed clutches of eggs have been considered. In 1941, at Orland, there were 3.66 eggs per completed clutch as compared with 3.69 for B. The difference is insignificant. There are data for both 1940 and 1941 for nests which were assigned in the field to brood I. For A, the values were 3.68 and 3.74 respectively per completed clutch as compared with the almost identical fecundity of 3.73 and 3.75 for B. These figures indicate that over a period of two years there was essentially no difference in fecundity of brood I between groups A and B. The fecundity of brood II in A during 1941 equaled 3.48 eggs as against 3.42 for B. These figures, while comparable between the two groups, are

consistently lower than those for brood I. A total of 17 eggs in 6 nests of the July brood at Orland suggests an even lower fecundity of 2.83 eggs per completed clutch in this brood.

There is identity between the total figures of fertility in groups A and B during 1941. The fertility of 437 eggs in A and 423 eggs in B was 95.7 per cent. 50 eggs of brood I at Orland that were carefully followed during 1940 gave a fertility of 96.0 per cent. In 1941 a larger sample of 344 fertile and 16 infertile eggs of brood I in this group result in a comparable figure of 95.6 per cent. During 1940 in B sampling of 89 eggs of brood I showed a fertility of 100 per cent. In the following year a sampling of 372 eggs in this brood gave a fertility of 96.2 per cent. In 1941, the fertility continued at the same level for brood II in A inasmuch as 98.5 percent of 65 eggs hatched. In B, there was a possibly significant decrease in fertility since 92.5 per cent of a sample of 47 eggs hatched. Fertility dropped to 81.8 per cent for the July brood at Orland upon the basis of a sample of only 11 eggs.

As a summary it may be stated that there is no difference between the total figures of fertility in groups A and B. The percentages of fertility of brood I are also similar in A and B. The fertility of brood II apparently dropped slightly in B, perhaps as a consequence of the smallness of sample. In A, the July brood fertility dropped markedly, although the sample is again too small to be of much significance.

A few interesting results appear in connection with an analysis of parasitism of red-wings by cowbirds. During 1940, in B, no cowbird eggs are known to have been deposited in nests of red-wings. In 1941, however, there were 9 cowbird eggs deposited in a similar number of red-wing nests in B, an incidence of almost 5 per cent of parasitized nests. There were 577 red-wing eggs deposited in the B nests; hence the percentage of

parasitism per red-wing egg is 1.6 per cent. Of these 9 eggs, there was a mortality of 8 eggs and 0 nestlings. One individual which was fledged gave a reproductive success of *Molothrus ater* in nests of *Agelaius phoeniceus* of 11.1 per cent. There was, in this instance, no mortality of red-wing eggs or nestlings associated with the parasitism. Four red-wing eggs which were deposited in this nest were also successful.

In 1940, at Orland, two cowbird eggs, an incidence of parasitism of 0.6 per cent, were deposited in a red-wing nest in which no eggs of red-wings had as yet been laid. These eggs did not develop since desertion of this nest followed without any deposition of red-wing eggs. The success of cowbird reproduction in this locality in 1940 is thus 0 per cent. During 1941, no cowbird eggs were deposited in A. This is in comparison with 563 eggs of red-wings which were deposited in nests of this locality. The possibility is suggested by these data that there may be an aggregate effect of numbers which retards or even prohibits the deposition of cowbird eggs in red-wing populations of high density. In view of the restricted incidence of cowbird parasitism and its apparent negligible effect upon red-wing mortality, it would appear that this factor is of relatively little importance in a consideration of the success of red-wing reproduction.

DISCUSSION

It is well to refer to Darling ('38) to get orientation for this discussion of the results with red-wings. In addition to the quotations given earlier, the following summarizing statements are helpful: (p. 3) "The thesis of this essay is that the social group and its magnitude, in birds which are gregarious at the breeding season, are themselves exteroceptive factors in the development and synchronization of reproductive condition in the members of individual pairs of birds and throughout the flock." (p. 89)

"The group of fourteen present in 1937 was successful in breeding but it would be unwise to select any number . . . as being the numerical threshold. Six birds did not breed in one year; fourteen did in the next." (p. 105) "I feel drawn to speculate for a moment here on the fate of very small populations of animals. It is often found that when the representatives of a species in any one habitat are reduced to very low numbers, breeding becomes irregular and the species disappears in spite of careful efforts which may have been made to restore it."

The further discussion centers about Darling's ('38) three suggestions concerning the effect of size of local breeding populations upon the breeding activity and reproductive success of colonial nesting birds. As was stated before, Darling's suggestions were to the effect that in the larger colony breeding starts earlier, there is greater synchronization of egg-laying, and group survival values are shown primarily because of failure of very small colonies even to lay eggs or a reduced span of helplessness on the part of the eggs and nestlings. In addition, there is Stresemann's ('28) suggestion concerning a greater survival value of the larger colonies by mass protection against predators.

RELATION OF COLONY SIZE TO ONSET OF BREEDING

Darling records that in 1936, the largest herring gullery (84-90 birds) which he watched began breeding 11 days before one with 20 birds while a colony of 2 pairs did not breed at all. In 1937, there was a lag of only 4 days between the largest colony and one of only 3 pairs, and the two larger colonies began breeding on the same day. In 1936, a colony of 72-80 black-backed gulls began breeding 8 days earlier than one of 18. The following year the difference was only two days between colonies of 120 and of 30 birds.

Roberts ('40) states that, in penguins, there appears to be no minimum threshold of numbers which is necessary to enable these forms to undergo a complete cycle of reproduction. A rough census of 137 colonies of Gentoo penguins (*Pygoscelis papua*) and Rockhopper penguins (*Eudyptes cristatus*), which ranged in size from 30 pairs to approximately 800,000 pairs, failed to give "any conclusive evidence that laying started earlier in the largest colonies, or that ovulation in the larger colonies was spread over a shorter period than in the small ones."

Fisher and Waterston ('41) have investigated the increase in numbers of breeding fulmars (*Fulmarus g. glacialis*) in the British Isles since 1878. It has been found that there is an average number of 4.4 years after a new breeding locality has been first populated by fulmars before any egg-laying is known. The possibility of a minimum threshold of numbers which is necessary for successful reproduction is suggested by these data. Egg-laying begins earlier in extensive than in small groups, although hatching and fledging tend to occur at about the same time in every colony.

Mayr ('41) investigated this point with red-winged blackbirds in four small swamps in New Jersey. In 1940 the five resident females in a brushy swamp laid their first eggs on May 20, 21, 22, 24 and 25 respectively. In a swamp with adequate cover, the 2 resident females laid their first eggs on May 24 and 25 or 26. In a similar swamp with one resident female, the first egg was laid on May 23. These data compare somewhat favorably with Darling's observations for gulls. A nearby larger swamp with poorer nesting sites but with a breeding population of 10-13 females, showed no red-wing eggs until May 26 or 27 (probable date). In my opinion Mayr has correctly interpreted the general situation to mean that ecological factors other than population size deter-

mined the earlier onset of breeding in the smaller as compared with the largest colony. With those colonies where the nesting sites are more nearly similar, Darling's generalization on this point has some support.

Similarly inclusive evidence is furnished by Fautin ('41b) who carefully followed the progress of nesting activities in two colonies of yellow-headed blackbirds in Utah. The larger colony contained 83 nesting females and about 35 males. Similar counts for the smaller colony were 40 and 12 respectively. Fautin says (p. 108), "The deposition of eggs began about the same time in both colonies." The first egg was recorded on May 7 in the larger colony and on May 8 in the smaller one. This difference of one day happens to be in line with Darling's generalization.

The writer's observations upon red-wings indicate that egg laying began two days earlier in 1940 in one of the smaller breeding populations than in the large colony at Orland. In 1941 there was a difference again of two days, this time in favor of the larger population so far as initial egg laying was concerned. The onset of general breeding started decidedly earlier in the larger colony in 1941.

From such evidence, it is impossible to conclude that, in these two species of marsh-nesting blackbirds, the onset of breeding is directly related to colony size. While such a conclusion may yet be reached when enough data are collected, the sampling observations to date do not permit such an inference to be drawn.

The question of effect of colony size upon the beginning and synchrony of breeding activities is a part of the broader problem of the role of exteroceptive factors such as courting display in mating. Howard ('29, '35) has recently presented an explanation of the survival value of these activities. His theory is that display constitutes a normal type of extrinsic stimulation

which intensifies sexual activity in a mated pair. If sexual activity is at a peak of intensity, a copulatory response may follow an ordinary stimulus of voice or appearance. Usually, however, an adequate synchronization of rhythms is obtained only by means of a further stimulus which is supplied by posturing. Frequently, if this stimulus is of sub-threshold intensity, there is a summation of attempts which establishes a copulatory reaction whereas otherwise a delayed or unsuccessful coition might result. The importance of an effective synchronization of male and female reproductive rhythms is expressed by Howard ('29) who says that "those pairs . . . in which the rhythms of reactions combine harmoniously will score a larger number of successful conjugations" than other pairs in which there is a weaker manifestation of display and posturing. It is the characteristics of highly integrated pairs, therefore, that will be perpetuated in the breeding population by natural selection. Marshall ('36, '42) also states that it is in this manner that the survival value of sexual display and adornment probably operates.

Darling ('38, p. 20) expresses the view that "although the immediate mate of opposite sex may be the most potent excitatory individual to reproductive condition, other birds of the same species, or even similar species, may play a decisive role if they are gregarious at the breeding season. Without the presence of others the individual pairs of birds may not complete the reproductive cycle to the limit of rearing young to the fledgling stage." (p. 96) "This finding is in keeping with expectations based on *theory of numerical thresholds and social stimulation*" (italics mine).

Behavior factors which might influence the onset and synchronization of breeding in colonies of red-wings include (1) song, which may be effective at a distance since it may be heard on a quiet day for as far as two miles (cf. Nuttall, 1840, cited

by Allen, '14). (2) The ordinary display of males by erecting feathers. (3) A spiraling and hovering flight by males which eventually ends in a zigzag descent into the marsh. Allen describes this accurately (p. 90) and continues: "A dozen or more birds may frequently be seen in the air at once, as they perform these evolutions. At this time, also, hovering at a much lower height is frequently indulged in." With a few quick strokes of his wings, the male vaults from his post into the air, and with quivering wings and flaming shoulders, gives vent to his pent-up passion in the 'scolding song.'" (4) The males drive resident females at first in a sort of frenzied pursuit and later follow her quietly.

Any effect of these various flying activities would be limited to the red-wings within visual range; vocalization might be effective at a greater distance. Such exteroceptive factors could operate in the beginning of breeding, in the pairing of individuals in similar phases of the reproductive cycle and in the synchronization of breeding processes within individual pairs of birds and throughout a flock.

RELATION OF COLONY SIZE TO SYNCHRONIZATION OF BREEDING

Darling's ('38) most convincing data, although by no means all of his information upon this point, have already been summarized. Roberts ('40) did not find convincing evidence that egg-laying in the larger colonies of penguins extended for a shorter period than in the smaller ones. On the other hand Fisher and Waterston ('41) record a slightly shorter period of egg-laying in large as opposed to small groups of fulmars. However, there do not appear to be any differences in the periods of hatching or fledging in relation to the magnitude of breeding population.

Fautin ('41b, p. 108) found that the duration of egg-laying in his larger colony of yellow-headed blackbirds lasted from May 7 to June 10; in his smaller

colony, the limiting dates were May 8 to June 22. The duration of laying was 11 days shorter in the larger colony. Fautin (p. 119) does not regard this difference as conclusive support of what he terms "Darling's Principle." Emlen ('41) has studied with care the breeding behavior of the Tricolored Red-wing (*A. tricolor*) and, upon the basis of his own observations and those of others, concludes (p. 211): "Tricolored Red-wings probably also depend to a certain extent on mutual stimulation from colony associates, for members of each nesting group show a marked simultaneity in breeding which is completely lacking as between different groups."

The red-wings at Orland similarly showed a higher degree of synchronization of breeding activity in brood I during the earlier part of the breeding season (see figure 2). This is better seen if attention is focused upon the bulk of egg-laying. In group B there was a sharp rise in egg production between May 27-June 4, at which time there was a decrease in such activity at Orland. To be sure the *total* time span for ovulation was greater in the larger colony at Orland than in the scattered smaller populations. As the season progressed, however, the environmental conditions became progressively dissimilar in the lots under consideration to such an extent that by the middle of June size of population is a factor of doubtful importance, in comparison with other elements of environmental control. If this analysis is correct, available data do suggest a higher synchronization of egg-laying activities which was associated with the greater density of breeding population at Orland during an important part of the 1941 breeding season.

THE RELATION OF POPULATION DENSITY TO REPRODUCTIVE SUCCESS

From some points of view this is the crux of the entire matter, since it raises the question of possible evolutionary sig-

nificance of population density in terms of survival values. Selection could favor either scattered or clustered nests or be entirely neutral as regards this factor. When or if the larger breeding population has survival value, this may result from the operation of one or more of the following factors: (1) tolerance for near neighbors in the face of a shortage of suitable nesting sites (cf. Allee, '31); (2) mass protection supplied by the "mobbing" of potential predators (cf. Stresemann, '28); (3) added protection on a percentage basis from the presence of larger numbers of prey (cf. Fautin, '41b); (4) heightened synchronization which shortens the more defenseless egg and nestling stages (cf. Darling, '38).

The present investigation has been concerned only incidentally with social tolerance. During 1940 and 1941 the red-wings did not populate all available cat-tail swamps to a certain toleration level and then overflow into marginal types of vegetation. Also in extensive cat-tail tracts which were studied in 1939, and which had contained a large population of nesting red-wings, the nests were not equally distributed but tended to occur in denser sub-colonies in the midst of less densely occupied areas of adequate cat-tail marsh.

As regards mass protection of eggs or nestlings, such behavior has long been recognized (cf. Stresemann, '28; Allee, '31). In the marsh at Orland, crows in particular were mobbed by grouped red-wings. The lack of cowbird parasitism at Orland in 1941 as contrasted with almost 5 per cent of parasitized nests in B may also be a measure of group protection. Since, however, the reproductive success was approximately the same in the different categories studied, such mass protection as existed was apparently offset by some unknown factor or factors.

It may be remembered that the only statistically significant difference in reproductive success was found in nests that were assigned in the field to brood

II. In this brood approximately 30 per cent more young were fledged at Orland than from the scattered B colonies. These results seem to be related to physical environmental differences. More specifically, it is believed that this difference is related to a drying up of the smaller marshes and ponds during the latter part of the breeding season while the marsh at Orland still held much water. The higher figure of mortality of brood II in B may be directly due to an increased availability of these eggs and nestlings to predators as a consequence of this environmental trend toward a terrestrial type of habitat; or it may possibly be an expression of a decrease in attentiveness of adults during the latter part of the breeding season in marshes and ponds which are progressively becoming dry. Either of these causes would tend to increase the mortality of eggs and nestlings in brood II in B. A continuation of these relationships probably permitted the July eggs to be deposited at Orland while continued breeding in the smaller marshes was effectively discouraged by their deterioration as breeding habitats. Lack ('33), in connection with investigations concerning the breeding of Arctic Terns (*Sterna paradisaea*), states that egg-laying does not normally take place unless certain conditions concerning the site and neighborhood of the nest are satisfied. This drying up of the marshes in group B could have affected the survival of nestlings by diminishing the available food supply. Allen ('14, p. 101) states that red-wing nestlings are fed on insect larvae or imagoes obtained in the marsh. The importance of an increased scarcity of such food, if indeed it was a factor at all, is lessened by the fact that loss was more severe in the egg stage than among the nestlings and by the further consideration that no dead bodies of starved nestlings were found.

Thus there is no evidence left that the larger breeding population of red-wings at Orland showed an increased repro-

ductive success which could be attributed to a higher synchrony of the breeding processes such as Darling ('38) observed for gulls.

Fautin ('41b, p. 118 ff.) found that the yellow-headed blackbirds which he studied hatched 75.7 per cent of 301 eggs laid in the larger colony as against 60.6 per cent of 142 eggs in the smaller colony. The larger colony was more disturbed by wind but the percentage of eggs destroyed, principally by predation, in the smaller colony was more than double that in the larger one. The final figure of success in producing fledglings was only 8 per cent greater for the larger colony. He discusses these results in connection with those of Darling's and adds the idea that the greater number of available prey in larger breeding colonies would tend to reduce the percentage lost by predation and so tend to give a higher survival value. This is true provided there are similar numbers of similarly effective predators in the situations which are being studied.

There is a possibility that even the best isolated pair of red-wings were not effectively isolated from other red-wings which were breeding in the general study area. If song is of importance in initiating and synchronizing breeding processes in these birds, and even though we halve the recorded distance which red-wing songs can be heard by man, none of the marshes studied was a mile away from larger-breeding populations and many of them were within visual distance of other colonies with displaying males. The validity of this suggestion cannot be estimated from available data. It is a complicating factor which should not be forgotten.

COMPARATIVE STUDIES IN REPRODUCTIVE SUCCESS

An analysis of the fate of every egg deposited in groups A and B during the breeding season of 1941 indicates that, of 1140 eggs which were laid in 25 study

localities, 675-681 individuals left nests as juveniles. This gives a mean reproductive success of approximately 59 per cent. This is rather high in comparison with numerous other published figures of reproductive success in red-wings. Nice ('41) has pointed out that there is no authenticity for a higher figure of 78 per cent which is cited by Kalmbach ('39) and Fautin ('41a) upon the basis of Allen's ('14) investigations of this species. Six other studies upon red-wings give figures of reproductive success which range down from the percentage here recorded. Incomplete results of Perkins ('28) indicate that 47 individuals, or 57 per cent, were fledged successfully out of a total number of 83 eggs in 24 nests of this species. M. Wood ('28) records a success of 21 fledglings (54 per cent) of 39 eggs which were deposited in 12 red-wing nests. In a neighboring swamp H. B. Wood ('38) found a success of 48 per cent from 73 eggs in a sample of 23 nests. Williams ('40) records 105 individuals, or 49 per cent fledged from 214 eggs deposited in 67 nests in a cat-tail marsh of about 10 acres in Ohio. These figures, gathered by different observers in diverse localities, are all of the same general order of magnitude.

Much lower nesting success has also been found in this species. Gabrielson ('15) on scanty data reports a success of only 8 nestlings, or 36 per cent, from 22 eggs which are known to have been deposited in 9 nests. Kalmbach ('39) records a very low figure of hatching of only 27 per cent in 281 eggs of red-wings in Louisiana; it is impossible that the percentage of fledging could have been in excess of 27 per cent. However, this reduced percentage of hatching is apparently explained by the fact that Kalmbach obtained his data in a locality where red-wings were breeding in abundance and where methods for their control were being worked out.

In a colony of yellow-headed blackbirds in Minnesota which was studied by

Roberts ('09), every egg or nestling in 36 nests was destroyed. The success of 130 eggs in this colony was thus nil. Fautin ('41a) in Utah found a success of 22 per cent in 443 eggs of the same species. These approach the values obtained by Gabrielson ('15) and Kalmbach ('39).

Nice ('37) has compiled data from 1994 eggs in six studies of reproductive success in a variety of open-nesting species of birds with altricial young. A mean percentage of fledging of 43 per cent was found in these studies. Nice's ('42) analysis of Kendeigh's ('42) compilation of reproductive efficiency for 2155 eggs in open nests of 11 species of altricial birds indicates a mean figure of success of 47 per cent in these latter investigations. Such data appear to suggest that red-wings reproduce somewhat more successfully than many other species of open nesting birds which construct their nests above ground level. This might be related to a lesser availability of red-wing eggs and nestlings to terrestrial predators which do not readily transgress an aquatic barrier such as is supplied by the borders of a marsh. However, this interpretation is not supported by the data on yellow-headed blackbirds which are also a marsh-inhabiting species. In addition, all such data, based on numbers of eggs laid, suffer from the serious lack of information concerning presence or absence of compensatory trends, such as might follow losses in early nestings.

The reproductive success found in this investigation in comparison with other studies upon red-wings may indicate an optimal set of environmental factors for red-wing reproduction during 1941 in the study area. There is a suggestion that any relation between population density and the reproduction of red-wings may have been obscured in the present investigation by such optimal conditions which existed for red-wings in breeding colonies of any magnitude. However, it appears that, if population

density is a factor in the reproduction of red-wings, it must necessarily operate in association with numerous other physical or biotic environmental influences. Apparently, one or more of these factors may frequently be of greater importance than colony size in influencing the progress of reproductive activities or the survival of red-wing eggs or nestlings.

AREA AND EDGE

There is an absence of any correlation in this study of reproductive success with density of breeding population or with the extent of margin or "edge" in any of the study localities. In 1941 about 155 individuals bred in an area of approximately 5.0 acres at Orland. This indicates a fairly high density of population of about 31 individuals per acre. There was an aggregate number of approximately 12.8 acres in the 24 restricted marshes and ponds of group B. Since 157-163 individuals reproduced in these localities during 1941, there is a much lower density of about 12.5 individuals per acre in this category of marshes and ponds. Nevertheless, reproduction was apparently equally successful under such conditions of a relatively sparse density of breeding population. As was pointed out earlier, the 1940 breeding populations were of the same order of magnitude as in the following year.

Only round figures of edge in the various study localities have been obtained in this investigation. However, it has been found that there were approximately 3000 linear feet of edge between *Typha* and open water or between *Typha* and more mesophytic types of vegetation at Orland. This is a relatively slight extent of edge for an area of approximately 5.0 acres. It is what one might expect in a roughly rectangular marsh which is composed mainly of a dense, uninterrupted stand of cat-tails. In the marshes and ponds of group B there were essentially 16,000 linear feet of edge of various sorts.

Vegetational boundaries of such diverse types as those between buttonbushes and open water and between bur reeds and mesophytic grasses have been added in order to obtain this figure. This treatment is necessary at least in a preliminary survey in measuring a factor which is apparently as complicated as habitat margin or as edge. Beecher ('42) found a correlation between the number of linear feet of edge in a variety of types of plant communities and the distribution of nests of numerous marsh-inhabiting as well as other species of birds. There does not appear to have been a critical investigation concerning a possible relationship between the extent of edge in a locality and the success of reproduction of such forms. Insofar as this factor has been analyzed in the present study, there is no apparent edge effect upon reproductive success in red-wings.

In the present study a few other interesting results have been obtained. Some of these will be discussed briefly as an indication of certain environmental factors which appear to influence the success of reproduction in red-wings. At Orland, cat-tails constituted the supports and the concealing vegetation for every nest in which eggs were deposited during 1941. A variety of plants fulfilled similar functions in the 24 marshes and ponds of B, and reproductive success in 1941 varied widely among the study localities of this group in relation to vegetational differences. Table I shows that *Sparganium* comprised the cover of relatively few nests of red-wings in this category of localities. Among nests which were constructed in this type of vegetation, however, it has been found that reproductive success was only 25 per cent. An analysis of the data from nests constructed in *Typha* indicates a higher success of 59.9 per cent. This is approximately equivalent to the total percentages of reproductive success which were given for groups A and B (table III). The success of red-

wing reproduction in two *Scirpus* localities and in a few brushy habitats of *Cephalanthus* and *Solanum* was in excess of 70 per cent. This high reproductive success is correlated apparently with the greater concealment of such nests. Among the various cat-tail marshes, there appears to have been less mortality in dense *Typha* localities than in open-water ponds in which the vegetation of cat-tails is reduced in extent or broken in its distribution. Approximately 56 per cent young were fledged successfully in nests which were built in open cat-tail situations while 63 per cent of the eggs in dense *Typha* localities were successful. These preliminary results strongly suggest a direct correlation of reproductive success with relative density of nesting cover among the various marshes and ponds of B and indicate a worthwhile problem for further study.

SUMMARY

1. The reproduction of an extensive breeding colony (A) of the Eastern Red-wing (*Agelaius p. phoeniceus*) has been compared with that of an equivalent number of individuals (B) breeding in small colonies in 24 marshes and ponds of restricted size.

2. The least synchronous total time span for ovulation was that of the colony of greatest magnitude. The total figures of reproductive success of groups A and B are essentially identical. These results are in contrast to those reported in gulls by Darling ('38).

3. Ovulation started earlier and there was a higher synchronization of the span of egg-laying of brood I in A than in B. These relations are similar to those found by Darling. However, the reproductive success of brood I was statistically similar in the category of smaller populations (B) and in the large population.

4. In brood II a higher one-day peak of ovulation in A than in B is again in conformity with Darling's results. In this case there was a longer span of egg-laying in A as well as similar per-

centages of double-broodedness in A and B. The success of reproduction of brood II was significantly higher in the larger colony.

5. There was a slight rise in egg production during July in the large breeding marsh. The reproductive success of the July eggs was very low.

6. No obvious correlation existed between reproductive success and the magnitude of breeding population in various minor groupings of the study localities of B.

7. The markedly higher success of reproduction of brood II in A than in B and the existence of a small July brood in group A are believed to be related to a drying up of the smaller localities during the latter part of the breeding season.

8. A mean reproductive success of 59 per cent is given which appears to be rather high in comparison with other published figures for altricial, open-nesting species which construct their nests above ground level.

9. There was an absence of any obvious correlation of reproductive success with density of breeding population per unit of area or with the extent of margin (edge) in the study localities.

10. A direct correlation of reproductive success with relative density of nesting cover among the various restricted marshes and ponds of B is suggested by preliminary results.

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